Mathematical Analysis of Sessile Metapopulation Model (Functional Equations in Mathematical Models)

AUTHOR(S):

Kamioka, Katumi

数理解析研究所講究録 1309 巻 2003 年 60-67

Mathematical Analysis of Sessile Metapopulation Model
(固着性メタ個体群モデルの数理解析)

Katumi, KAMIOKA (神岡 勝見)
Department of Mathematical Sciences, University of Tokyo
(東京大学大学院数理科学研究科)

1 Introduction

A metapopulation (such as *barnacles*) consists of many habitats for sessile adults and the planktonic larvae. The larvae are produced from all the local habitats, which are mixed in a common larval pool. The larvae then return to settle on vacant space in a local habitat. The local population is regulated by the death rate of adults in each habitat depend and by the settlement rate into vacant space. The settlement rate into a habitat on the amount of vacant space provides the density dependent competition among adult organisms and it leads to population regulation.

Under those observations, Iwasa and Roughgarden [1][2] have proposed a mathematical model. And they examine it numerically or quantitatively.

In this paper, we consider the case that two kinds of species and two local hatitats exist. We define some new threshold parameters. Using them, we argue the existence of the steady states and their stability.

2 The model and steady states

Let P_{ij} be the density of adults of species i living in local hatitat j. In the following we use the index i, j to indicate the species i and the local hatitat j. Then the dynamics of P_{ij} is determined by the loss of adults due to mortality μ_{ij} and the settlement of larvae into the local habitat:

$$\frac{d}{dt}P_{ij}(t) = -\mu_{ij}P_{ij}(t) + c_{ij}(Q_j - S_j(t))L_i(t). \tag{2.1}$$

The second term of (2.1) is the rate of larval settlement which is proportional to the accessibility c_{ij} and the vacant space, total space minus occupied space

$Q_j - S_j(t)$, where the occupied space is defined as

$$S_j(t) := \sum_{i=1}^{2} \gamma_{ij} P_{ij}(t) \tag{2.2}$$

and γ_{ij} is the area occupied by a single individual. The number of larvae of species i in the larval pool, denoted by L_i, follows

$$\frac{d}{dt} L_i(t) = -v_i L_i(t) - \sum_{j=1}^{2} c_{ij}(Q_j - S_j(t)) L_i(t) + \sum_{j=1}^{2} m_{ij} P_{ij}(t). \tag{2.3}$$

The first and second term of (2.3) are the loss of larvae due to mortality v_i and the settlement. The third term is the sum of production of larvae by adults living in each local habitat with fertility m_{ij}.

The steady states are solved as roots of the hatitat derived from (2.1)-(2.3):

$$0 = -\mu_{ij} P^*_{ij} + c_{ij}(Q_j - S^*_j) L^*_i, \tag{2.4}$$

$$0 = -v_i L^*_i - \sum_{j=1}^{2} c_{ij}(Q_j - S^*_j) L^*_i + \sum_{j=1}^{2} m_{ij} P^*_{ij}, \tag{2.5}$$

$$S^*_j = \sum_{i=1}^{2} \gamma_{ij} P^*_{ij}, \tag{2.6}$$

where $i, j = 1, 2$. The symbols with an asterisk indicate the values at a steady state. It is easily seen that the trivial steady state, the absence of organisms, exists for all arbitrary parameters.

For the sake of simplicity, we introduce α_{ij} as abbreviation defined as

$$\alpha_{ij} := \frac{\gamma_{ij} c_{ij}}{\mu_{ij}}.$$

α_{ij} represents the expected basal area of a larva of species i that settles in local hatitat j. By the use of this notation and the elimination of P^*_{ij}, (2.4)-(2.6) are reduced to a hatitat of L^*_i and S^*_j:

$$0 = L^*_i \left\{ v_i + \sum_{j=1}^{2} c_{ij}(Q_j - S^*_j) \right\} \{\Psi_i(S^*_1, S^*_2) - 1\}, \tag{2.7}$$

$$S^*_j = \sum_{i=1}^{2} \alpha_{ij}(Q_i - S^*_i) L^*_i, \tag{2.8}$$

where $i, j = 1, 2$. The functions Ψ_i introduced in (2.7) are given by

$$\Psi_i(\xi_1, \xi_2) := \frac{\sum_{j=1}^{2} \frac{m_{ij} c_{ij}}{\mu_{ij}} (Q_j - \xi_j)}{v_i + \sum_{j=1}^{2} c_{ij} (Q_j - \xi_j)}.$$

We shall show the existence of the non-trivial steady state for species 1 such that only species 1 is present. And the case for species 2 can be shown along the same manner.

Let $L_1^* > 0$ and $L_2^* = 0$, then (2.7)-(2.8) are reduced to

$$\Psi_1(S_1^*, S_2^*) = 1, \tag{2.9}$$

$$S_j^* = \alpha_{1j}(Q_j - S_j^*)L_1^*, \ j = 1, 2. \tag{2.10}$$

Here we adopt the following assumption:

Assumption 1. *$\Psi_i, i = 1, 2$, are strictly monotonically decreasing functions with respect to both variables.*

We introduce new parameters which represents the expected number of larvae reproduced by a larva:

$$R_{0i} := \Psi_i(0, 0) = \frac{\sum_{j=1}^{2} \frac{m_{ij} c_{ij}}{\mu_{ij}} Q_j}{v_i + \sum_{j=1}^{2} c_{ij} Q_j}.$$

R_{0i} is called the *basic reproduction number* for species i. Hence we can prove the next threshold theorem:

Theorem 2. *Under Assumption 1, if $R_{01} \square 1$, only the trivial steady state exists. And if $R_{01} > 1$, the non-trivial single-species' steady state uniquely exists.*

Proof. Substituting (2.10) into (2.9), we obtain the quadratic equation for L_1^*:

$$\phi(L_1^*) = 0, \tag{2.11}$$

$$\begin{aligned}\phi(L_1^*) &:= v_1\alpha_{11}\alpha_{12}L_1^{*2} + \{v_1(\alpha_{11}+\alpha_{12}) + c_{11}Q_1\alpha_{12} + c_{12}Q_2\alpha_{11}\} \\ &\times \left\{1 - \Psi_1(\frac{\alpha_{12}Q_1}{\alpha_{11}+\alpha_{12}}, \frac{\alpha_{11}Q_2}{\alpha_{11}+\alpha_{12}})\right\} L_1^* \\ &+(v_1 + c_{11}Q_1 + c_{12}Q_2)(1 - R_{01}). \end{aligned} \tag{2.12}$$

From Assumption 1, we have

$$\Psi_1(\frac{\alpha_{12}Q_1}{\alpha_{11}+\alpha_{12}}, \frac{\alpha_{11}Q_2}{\alpha_{11}+\alpha_{12}}) < \Psi_1(0,0) = R_{01}.$$

Then the coefficient of the first degree of (2.12) is non-negative and

$$\phi(0) = (v_1 + c_{11}Q_1 + c_{12}Q_2)(1 - R_{01}) > 0$$

if $R_{01} \square 1$. Then (2.11) has no positive root. On the other hand, $\phi(0) < 0$ if $R_{01} > 1$. This leads to the uniquely existence of the positive steady state and it is uniquely determined as a larger root of (2.11). □

3 Local and global stability of steady states

The local stability is studied by linearizing the basic equation around a steady state $(P_{11}^*, P_{12}^*, P_{21}^*, P_{22}^*, L_1^*, L_2^*)$. The linearized matrix is a 6×6 matrix and is given by

$$A := \begin{pmatrix} -\mu_{11} - c_{11}L_1^*\gamma_{11} & 0 & -c_{11}L_1^*\gamma_{21} \\ 0 & -\mu_{12} - c_{12}L_1^*\gamma_{12} & 0 \\ -c_{21}L_2^*\gamma_{11} & 0 & -\mu_{21} - c_{21}L_2^*\gamma_{21} \\ 0 & -c_{22}L_2^*\gamma_{12} & 0 \\ m_{11} + c_{11}L_1^*\gamma_{11} & m_{12} + c_{12}L_1^*\gamma_{12} & c_{11}L_1^*\gamma_{21} \\ c_{21}L_2^*\gamma_{11} & c_{22}L_2^*\gamma_{12} & m_{21} + c_{21}L_2^*\gamma_{21} \end{pmatrix}$$

$$\begin{pmatrix} 0 & c_{11}(Q_1 - S_1^*) & 0 \\ -c_{12}L_1^*\gamma_{22} & c_{12}(Q_2 - S_2^*) & 0 \\ 0 & 0 & c_{21}(Q_1 - S_1^*) \\ -\mu_{22} - c_{22}L_2^*\gamma_{22} & 0 & c_{22}(Q_2 - S_2^*) \\ c_{12}L_1^*\gamma_{22} & -v_1 - \sum_{j=1}^{2} c_{1j}(Q_j - S_j^*) & 0 \\ m_{22} + c_{22}L_2^*\gamma_{22} & 0 & -v_2 - \sum_{j=1}^{2} c_{2j}(Q_j - S_j^*) \end{pmatrix}.$$

From now, we investigate the eigenvalues of matrix A to study the local stability of steady states. The characteristic equation for the matrix A is

$$\det(\lambda I - A) = 0, \tag{3.1}$$

where λ denotes the complex number and I the 6×6 identity matrix. Substituting the trivial steady state $(P_{11}^*, P_{12}^*, P_{21}^*, P_{22}^*, L_1^*, L_2^*) = (0,0,0,0,0,0)$ into (3.1) and using standard rules to simplify the determinant of a matrix, we can rewrite (3.1) as

$$f_1(\lambda) f_2(\lambda) = 0, \tag{3.2}$$

where

$$\begin{aligned} f_i(\lambda) \;:=\; & \left(\lambda + v_i + \sum_{j=1}^{2} c_{ij} Q_j\right) \prod_{j=1}^{2} (\lambda + \mu_{ij}) - c_{i1} Q_1 m_{i1} (\lambda + \mu_{i2}) \\ & - c_{i2} Q_2 m_{i2} (\lambda + \mu_{i1}). \end{aligned} \tag{3.3}$$

We need not to assume Assumption 1 to show the following theorem.

Theorem 3. *If* $\max_{i=1,2} R_{0i} < 1$, *then the trivial steady state is locally asymptotically stable, whereas it is unstable if* $\max_{i=1,2} R_{0i} > 1$.

Proof. To show the sign of roots is what only we have to do. Without loss of generarity, we can assume $R_{01} \geq R_{02}$ and $\mu_{11} > \mu_{12}$. Then we see that

$$\begin{aligned} &\lim_{\lambda \to -\infty} f_1(\lambda) = -\infty, \\ &f_1(-\mu_{11}) = -c_{11} Q_1 m_{11} (\mu_{12} - \mu_{11}) > 0, \\ &f_1(-\mu_{12}) = -c_{12} Q_2 m_{12} (\mu_{11} - \mu_{12}) < 0. \end{aligned}$$

According to these relations, we have two negative roots of $f_1(\lambda) = 0$ which lie in $(-\infty, -\mu_{11})$ and $(-\mu_{11}, -\mu_{12})$. Next we check the sign of $f_1(0)$. Substituting $\lambda = 0$ into (3.3), we have

$$f_1(0) = \mu_{11}\mu_{12} \left(v_1 + \sum_{j=1}^{2} c_{1j} Q_j\right) (1 - R_{01}).$$

Since $\lim_{\lambda \to +\infty} f_1(\lambda) = +\infty$, it follows that the largest root lies in $(-\mu_{12}, 0)$ if $R_{01} < 1$ or in $(0, +\infty)$ if $R_{01} > 1$. Therefore all roots are negative if $R_{01} < 1$, and if $R_{01} > 1$ then (3.3) has a positive root. The remaining cases are established by applying the similar manner, too. This completes the

In the following we shall show the local stability for non-trivial single-species' steady state of species 1. We suppose $R_{01} > 1$. The characteristic equation (3.1) for $(P_{11}^*, P_{12}^*, 0, 0, L_1^*, 0)$ becomes the product of two functions just like (3.2), which are given as follows:

$$\begin{aligned} f_1(\lambda) &:= (\lambda + v_1)\prod_{j=1}^{2}(\lambda + \mu_{1j}^*) + c_{11}(Q_1 - S_1^*)(\lambda + \mu_{12}^*)(\lambda + \mu_{11} - m_{11}) \\ &\quad + c_{12}(Q_2 - S_2^*)(\lambda + \mu_{11}^*)(\lambda + \mu_{12} - m_{12}), \qquad (3.4) \\ f_2(\lambda) &:= (\lambda + v_2)\prod_{j=1}^{2}(\lambda + \mu_{2j}) + c_{21}(Q_1 - S_1^*)(\lambda + \mu_{22})(\lambda + \mu_{21} - m_{21}) \\ &\quad + c_{22}(Q_2 - S_2^*)(\lambda + \mu_{21})(\lambda + \mu_{22} - m_{22}), \qquad (3.5) \end{aligned}$$

where $\mu_{1j}^* := \mu_{1j} + \gamma_{1j}c_{1j}L_1^*$. Here we introduce another significant parameter defined by $R_{02}^* := \Psi_2(S_1^*, S_2^*)$. We remark that S_j^* is the occupied area of only species 1. This is the *reproduction number* for species 2 in the condition that the system is in the non-trivial single-species' steady state of species 1.

Under Assumption 1, the next theorem holds.

Theorem 4. *If $R_{02}^* < 1$ then the non-trivial single-species' steady state is locally asymptotically stable. And it is unstable if $R_{02}^* > 1$.*

This theorem will be shown by the following Lemma 5 and Lemma 6.

Lemma 5. *$f_1(\lambda) = 0$ has three negative roots.*

Proof. Since almost part of this proof is similar to it of Theorem 3, then we only check the sign of $f_1(0)$. From Assumption 1 and (2.9), we obtain

$$\Psi_1\left(\frac{\gamma_{11}c_{11}L_1^*Q_1 + \mu_{11}S_1^*}{\mu_{11}^*}, \frac{\gamma_{12}c_{12}L_1^*Q_2 + \mu_{12}S_2^*}{\mu_{12}^*}\right) < \Psi_1(S_1^*, S_2^*) = 1.$$

Then it follows that

$$\begin{aligned} f_1(0) &= \{v_1\mu_{11}^*\mu_{12}^* + c_{11}\mu_{11}\mu_{12}^*(Q_1 - S_1^*) + c_{12}\mu_{12}\mu_{11}^*(Q_2 - S_2^*)\} \\ &\quad \times \left\{1 - \Psi_1\left(\frac{\gamma_{11}c_{11}L_1^*Q_1 + \mu_{11}S_1^*}{\mu_{11}^*}, \frac{\gamma_{12}c_{12}L_1^*Q_2 + \mu_{12}S_2^*}{\mu_{12}^*}\right)\right\} > 0. \end{aligned}$$

Therefore our claim follows. □

Lemma 6. *If $R_{02}^* < 1$ then three negative roots of $f_2(\lambda) = 0$ are negative, and if $R_{02}^* > 1$ then two roots are negtive and the largest one is positive.*

Proof. By the same manner as the part of the proof of Theorem 3, it is shown that $f_2(\lambda)$ always has two negative roots whether $R_{02}^* > 1$ or not. Therefore we only show the sign of the largest root, which is determined by it of $f_2(0)$ since $\lim_{\lambda \to +\infty} f_2(\lambda) = +\infty$ holds. As we substitute $\lambda = 0$ into (3.5), then we have

$$f_2(0) = \mu_{21}\mu_{22} \left\{ v_2 + \prod_{j=1}^{2} c_{2j}(Q_j - S_j^*) \right\} \{1 - R_{02}^*\}.$$

So all roots are negative if $R_{02}^* < 1$. On the other hand, the largest root is positive if $R_{02}^* > 1$. This completes the proof. □

From Lemma 5 and Lemma 6, we completes the proof of Theorem 4. We notice that the same result of Theorem 4 holds for species 2.

Finally, we are going to establish the global stability of the trivial steady state. We again assume Assumption 1 then we have the following theorem:

Theorem 7. *If* $\max\{R_{01}, R_{02}\}$ □ 1, *the trivial steady state is globally asymptotically stable.*

Proof. It is sufficient to show the existence of a Liapunov function. In fact, it is made as the following:

$$V(\mathbb{P}, \mathbb{L}) := \sum_{i,j=1,2} \frac{m_{ij}}{\mu_{ij}} P_{ij} + \sum_{i=1}^{2} L_i, \tag{3.6}$$

where $\mathbb{P} = (P_{11}, P_{12}, P_{21}, P_{22}), \mathbb{L} = (L_1, L_2)$. The first term of (3.6) represents the expected number of current larvae which are going to be released by the current adults and the second term does the number of current larvae. And (3.6) is defined on the bounded set $\Omega \subset \mathbb{R}^6$:

$$\Omega := \{(\mathbb{P}, \mathbb{L}) \in \mathbb{R}^6; P_{ij} \geq 0, S_j \text{ □ } Q_j, L_i \geq 0, i, j = 1, 2\}.$$

This set is positively invariant with respect to the flow defined by (2.1)-(2.3). From the Assumption 1, the time derivative of V along solution of (2.1)-(2.3)

is as follows:

$$\begin{aligned}\dot{V}(\mathbb{P}(t),\mathbb{L}(t)) &= \sum_{i=1}^{2} L_i(t)\left\{v_i+\sum_{j=1}^{2} c_{ij}(Q_j-S_j(t))\right\}\{\Psi_i(S_1(t),S_2(t))-1\}\\ &\square \sum_{i=1}^{2} L_i(t)\left\{v_i+\sum_{j=1}^{2} c_{ij}(Q_j-S_j(t))\right\}\{R_{0i}-1\}.\end{aligned}$$

By the LaSalle invariance principle, it follows that the trivial steady state is globally asymptotically stable if $\max\{R_{01}, R_{02}\}$ □ 1. □

4 Discussion

The existence, the local and global stability of steady states are discussed. Most importantly, we have shown the definite expression of the basic reproduction numbes, R_{0i}, and the reproduction numbers, R^*_{0i} as threshold parameters. They governs whether or not the steady state is locally or globally stable. Especially we may call R^*_{0i} an *invasion* parameter, for R^*_{0i} is the reproduction number of species i under the other species.

There are still some challenging questions which need to be studied for system (2.1)-(2.3). We will have to consider the case that Assumption 1 does not hold though it is adopted to avoid the non-uniqueness of the non-trivial steady state. It is of more biologically significance to consider the case of co-existence. We leave this for future work.

References

[1] Y. Iwasa, J. Roughgarden, Dynamics of a metapopulation with space-limited subpopulations, Theor. Popu. Bio. 29 (1986) 235-261.

[2] Y. Iwasa, J. Roughgarden, Interspecific competition among metapopulations with space-limited subpopulations, Theor. Popu. Bio. 30 (1986) 194-214.